BODY TEMPERATURES IN SOME AUSTRALIAN MAMMALS. III. CETACEA¹ (MEGAPTERA)

PETER MORRISON

School of Physiology, University of Queensland, Brisbane, and Departments of Zoology and of Physiology, University of Wisconsin, Madison 6, Wisconsin

Whales have always attracted popular interest both as the largest animals and as a valuable object in commerce, but their size and wide range make approach difficult and have discouraged the accumulation of reliable information about them. Although their unique size lends interest to any aspect of their life, the topic of body temperature to be considered here bears on a point of particular interest in view both of the general relations between energy production, mass, and heat dissipation in mammals, and the special problems of aquatic mammals (Scholander and Schevill, 1955).

Because of "technical" difficulties, body temperatures have only conveniently been measured on dead whales, although advances in telemetry may offer another approach in the future. Ordinarily one would consider a measurement obtained an hour after death to be quite questionable and one obtained ten hours after death to be of no value at all. However, the enormous bulk of the whale greatly reduces heat dissipation. The covering layer of blubber constitutes an effective insulation and this, together with the high heat capacity of the system and the low relative surface area, greatly reduces heat loss. It has been estimated that a 24 M. (122-ton) whale has a surface of 275 M.² or only 23 cm.²/kg. (Laurie, 1933). This is a tenth of the value in man and less than a hundredth of that in a mouse. Of course, in the living animal most of this reduction in surface is compensated for by the (presumed) lower metabolic rate in the whale, so that the metabolic output per unit of body surface may differ by no more than a factor of three in the largest and smallest mammals.²

In practice, it has been long known that whales do cool slowly after death. For example, Guldberg (1885) reported a temperature of 34° in a fin whale three days after death. Cockrill (1951) described a whale fillet of about three tons which was towed for 21 hours in antarctic waters with a resultant fall of only 1° F. in deep temperature. Ash (personal communication) has "observed

¹ This study was carried out with assistance from the Guggenheim Foundation and the U. S. Educational Foundation in Australia, and would not have been possible without the wholehearted assistance of Dr. Victor Macfarlane of the School of Physiology at Brisbane. I am indebted to Dr. Masaharu Nishiwaki of The Whales Research Institute (Tokyo), to Dr. J. G. Sharp of The Low Temperature Research Station (Cambridge) and to Dr. C. E. Ash of United Whalers Ltd. (London) for supplying very interesting unpublished records of whale temperatures; and to Dr. Clinton Woolsey for similar data on a porpoise. I also appreciate the kindness of Dr. William E. Schevill in checking the manuscript and nomenclature.

² This represents the difference between the two weight functions for surface $(A = kW^{.667})$ and metabolism $(M = kW^{.754})$ so that $M/A = kW^{0.067}$. Taken over the shrew-to-whale weightspan $(3 \rightarrow 10^8 \text{ g.})$ this amounts to a factor of $3\times$. Over the mouse-to-elephant span $(20 \rightarrow 4 \times 10^6 \text{ g.})$ the factor is 2.2.

BODY TEMPERATURE IN MEGAPTERA

a fillet of meat (longissimus dorsi) maintain a steady temperature of 35° C. in the interior for 15 hours *post mortem*." Robinson *et al.* (1953) summarized data to show (p. 6) that "up to 24 hours after death, whale muscle does not lose heat to a significant extent." Indeed, Irving and Krogh (1954) have reported that even in the very much smaller (though well insulated) reindeer and caribou, and under the extreme ambient conditions of -45° C. in strong wind, there was no demonstrable fall in deep body temperature in the hour following death.

MATERIALS AND METHODS

Observations were made on 20 recently killed humpback whales (*Megaptera* novacangliae) at coastal whaling stations on Moreton Island in southern Queensland just off Brisbane and in Byron Bay in northern New South Wales, the easternmost point in Australia. We are indebted to the respective concerns. Whale Products, Ltd. and the Byron Whaling Co., Ltd., for their cooperation in making these studies possible. Measurements on four whales (No. 512, X, Y, and Z) were kindly made by Dr. K. C. Robbins of the CSIRO. At both these locations whales are killed close offshore from small vessels similar to those used in the larger antarctic whaling operations. But instead of being picked up by a large "factory" ship they are towed to fixed shore installations where the carcasses are cut up and rendered. The period between death and disposal varies from one to sixteen hours, depending on the towing distance, the weather conditions, and the work load. These whales ranged from 35 to 45 feet in length and were considered to carry roughly a ton of weight for each foot in length.

Temperatures were measured with copper-constantan thermocouples using a Cambridge thermocouple-potentiometer unit. This provided connections for manual switching between six thermocouples. One of these was used as a reference junction for calibration of the instrument against a mercury thermometer in a small Dewar flask. The other five were fixed at twelve-inch intervals along a one-inch stainless steel tube. The plastic-coated thermocouple wires were further protected by an outer small plastic tube, which was led down the inside of the probe and brought out at the appropriate point through a small hole. The junction was thus exposed on the outer surface of the probe (although still protected by the plastic cover), and the far end was run through another hole and secured inside by knotting. A demountable harpoon head with tempered cutting edges was fixed to the shaft to allow penetration through the tissues. The first thermocouple lay two inches above the head, and the fifth, four feet higher; but all thermocouple wires were of the same length. In preliminary tests it was not possible to check the thermocouples against one another to better than 1° C. But on two occasions during measurements on whales the heart was penetrated so that the hollow thermocouple probe carried a stream of blood out of the body. Under these conditions, values for the several couples all check each other within 0.1° C.

In one series of measurements, made from the deck of the whale chaser immediately after capture, approach was limited to the more posterior regions and insertions could be made only with great difficulty. Because of unfavorable weather conditions, the carcass rose three to six feet with each swell, and on several occasions the one-inch steel probe was bent to a right angle against the side of the vessel. Most of the measurements, however, were carried out after the

whales had been towed ashore and under these circumstances the probe could be readily positioned in any part of the body. Insertions were normally made from the ventral surface near the midline, with the last thermocouple set just below the surface, or when further penetration was stopped by bone. The various insertion positions are diagramed in Figure 1.



FIGURE 1. Humpback whale profile showing axial positions for thermometer insertions. F, flipper; U, umbilicus; G, genital opening.

Results

In each case, values from the four or five thermocouples provided a temperature profile through the whale. The anticipated sequence, that most commonly



FIGURE 2. Temperature-depth profiles at various axial positions in whale No. 502, showing normal gradients.

observed, found the innermost couple (#1) or perhaps the next (#2) at the highest temperature, with the other values decreasing uniformly as the surface was approached. A representative set of such data is shown in Figure 2.

However, sometimes quite abrupt changes were observed between adjacent regions; and even reverse gradients were seen (Fig. 3). The reason for these marked changes in temperature was not immediately evident, although a somewhat similar lability was described by Nishiwaki (personal communication) in successive measurements on whales taken during Japanese operations in the Antarctic. Substantial changes in temperature either over short distances or short time periods seem incompatible with either a thermoregulated or an inert body of this bulk. The explanation appears to lie in changes which occur during capture. At this time, the whale is first secured by a harpoon with an attached line; and a subsequent shot carrying an explosive charge kills the animal. Sometimes several such shots may be required. These wounds can admit sea water into the animal; and during their death throes quantities of sea water may be ingested, taken into the rectum or vagina, or aspirated into the lungs.³ Accordingly, the temperature profile through positions III and V in Figure 3 must reflect the presence of a mass of cold water, in this case at a depth of 1.5 to 2.5 feet from the surface.



FIGURE 3. Temperature-depth profiles at various axial positions in whale No. 499, showing inverted gradients.

³ Such circumstances were described by men of the flensing crew.

Body temperatures also varied markedly with the location of the insertion along the body axis (Fig. 4). Highest values were found to the posterior, and a point of insertion midway between the umbilicus and the genital opening consistently gave the highest readings. At this point, the inner thermocouples would lie in or near the large muscle masses along the vertebrae. Mean maximum values at the various insertion positions are shown in Figure 4. Values at the level of the heart (position II) were somewhat higher than the next point to the rear, but averaged 2° lower than the maximum for the animal (position V).



FIGURE 4. Maximum body temperatures at various axial positions in four individuals. Heavy curve through crossed circles represents an average for all values calculated from means for pairs of values from two axial positions (all axial positions were not measured on all whales).

Complete data for these maximum temperatures along the axis are presented in Table I. Data for the entire series of whales, including the maximum temperature observed anywhere in the body, are summarized in Table II. No relation is seen between body temperature and either sex or length. Nor is there a correlation with the time after death, mean values after 2, 8, and 14 hours differing by only 0.2° C.

Average values for all points in each transect are presented in Table III. It is of interest that, even though position V always produced the highest single temperature, the mean value along this transect was lower than that at either the genital or the umbilical position on each side.

BODY TEMPERATURE IN MEGAPTERA

Whale	18.11	III	IV	V	VI & VII
492	35.2	35,6	35.6	_	
493	34.8	34.4	34.1		35.9
494		35.2			
498		32.1		36.3	
499	34.3	33.0		35.5	34.9
500	34.2	32.5		36.3	
501	33.7	33.5		35.8	33.5
502	32.6	31.5		35.3	34.6
503	34.9		35.1		35.3
512				36.1	
X				36.2	
Y				36.8	
Z				37.1	
В	34.5	36.1		35.3	35.4
С				35.0	
D	34.0	33.7			34.5
G			37.3		37.7
Н					36.8
I	35.7	35.8		36.3	34.3
J	34.9			34.9	34.2
Mean values	34.4	33.9	35.5	35.8	35.2
	(11)	(11)	(4)	(14)	(11)
Ave. depth (ft.)	2.7	3.8	3.7	3.3	2.8

TABLE I

Maximum temperatures at various axial positions

DISCUSSION

This study has shown that there may be considerable variation in temperature in different parts of the whale's body as measured after capture by commercial procedures. Some of this variation appears to be an artifact resulting from the intake of cold sea water into the body. However, one may minimize this error, as was done, by multiple testing to identify and avoid any "cold spots." But, with this precaution taken, there still remain substantial differences in the maximum temperatures along the body axis. Such axial temperature gradients are not uncommon among other mammals and may be quite prominent in some special situations such as arousal from hibernation; but the region of highest temperature is always near the heart and liver, with values declining to the rear. In the whale we see the reverse situation, with the higher values at the rear and lower values to the front. Values in the heart itself are not the lowest, but average 1.5° C. below the maximum. This may reflect a different balance in this large animal between the heat production in the muscle mass and that in the visceral organs. In considering this question, it would be very useful to have values for brain temperatures in whales and to have axial distributions in smaller cetaceans, but neither are available. However, measurements on the small killer whale (Orcinus) by Portier (1908) and on the seal (Phoca) by Scholander et al. (1942) gave higher brain temperatures than visceral temperatures. Another possibility to account for this axial gradient is extra heat production by the

TABLE H

Whale	Sex	Length ft.	Hours dead	Тв °C.
В	5	37	5	36.1
C			0.5	35.0
D			0.5	34.5
G			1	37.7
H			0.8	36.8
1			5.5	36,3
I			2.3	34.9
			2.2	35.9(7)**
492	d	40	8	35.6*
493	⊲്	35	7	35.9*
494	Ŷ	33	7	35.2*
503	്	35	7	35.3*
X	Ŷ	34	8	36.2
Y	ę	33	8	36.8
Z	Ŷ	36	8	37.1
			7.6	36.1(7)***
512	Ŷ	38	17	36.1
498	്	41	11	36.3
499	Ŷ	43	11	35.5
500	Ŷ	42	18	36.3
501	~	39	14	35.8
502	٥٦	38	13	35.3
			14	35.9(6)***
				36.0(20)

Maximum body temperatures in humpback whales

* "U-G" position not measured; may average 0.4° low. ** Whales from Byron Bay. *** Whales from Moreton Island.

Table 1		1
---------	--	---

Average body temperatures at various axial positions*

Whale	I or II Flippers**	III FU.	IV Umbilicus	V UG.	VI Genital
492 493 494	(35.2) 34.4	35.1 33.6 34.8	35.4 33.5		35.3
498 499 500	32.7	30.8 31.5		35.7 32.5	34.9
501 502 503	(33.7) (32.2) 34.1	32.8 31.1	34.7	32.4 33.8	32.1 33.4 34.3
	33.3	33.0	34.5	33.8	34.2

* 250 temperatures on 21 whales. ** Parenthesized values at flippers; others 2-3 feet behind at heart.

intestinal bacteria. In the largest land mammal, the elephant, the rectal temperature is suggested to be higher than the rest of the body because of this effect (Benedict, 1936). However, as carnivores, the whales should be less subject to this influence; and Robinson *et al.* (1953) report a very low bacterial content in the feces, perhaps $10^{-3}-10^{-6}$ times that in most fecal material. But, whatever the bacterial calorification, its effect would be enhanced by the large volume available and the whale's lower metabolic rate.

The data of Nishiwaki referred to above show some striking declines in temperature over relatively short periods. Indeed, the average decline for a series of whales is almost 3° /hr. (Fig. 5). It seems impossible to account for this except as a local cooling effect of water taken into the body at the point of measurement.

Equally striking are three curves where the temperature increased sharply instead of decreasing. One wonders if these may represent the phenomenon of



FIGURE 5. Temperature changes in dead whales from data of M. Nishiwaki (personal communication). Heavy curve and crossed symbols represent average of all data. Other curves illustrate rapid transitions of temperature.

"burning," a sharp increase in the dead whale's temperature described by whalers, which may be attributable to an explosive bacterial proliferation through the tissues. Under certain conditions, anaerobic bacteria may be widely distributed throughout the animal, apparently carried from the gut through the blood stream (Robinson *et al.*, 1953). I know of no actual temperature measurements which describe this phenomenon, although Kanwisher and Leivestad (1957) have reported an increase of 0.3° /hr. over an 8-hour period in one whale. The observed increases of 4 to 5° /hr. (Fig. 5) represent about 1 cc. O_2 /g. hr. or more than ten times the (predicted) basal heat production of the whale. The observed maxima near 40° (Fig. 5) may seem rather low to justify the impression of "burning," but it should be kept in mind that such comments are made by men acclimated to polar conditions. A temperature field of this size and intensity set in an icy sea could well feel uncomfortably hot to these observers.

Hours dead**	T B***	Range [†]	Values††
1-4	34.5	32-38	54
5-6	34.5	33-38	51
7 - 8	34.6	32-37	87
9-10	34.7	33-37	90
11-12	34.8	33-37	81
13-14	34.8	33-37	46
15 - 17	35.1	33–37	81
1-17	34.7	32-38	490

TABLE IV Whale temperatures by F. H. Addison*

* Unpublished Ministry of Food Report, "Antarctic Whaling Expedition, 1949–50"; personal communication from Dr. J. G. Sharp.

** Observations made on deck of factory ship.

*** "The highest meat temperature is invariably obtained of the longissimus dorsi, the best site being the middle part of the muscles adjacent to the lumbar vertebrae."

 \dagger The wide range reflects the large samples. These data showed a normal distribution with a standard deviation of 0.9° C. (See Fig. 6.)

 \dagger The bulk of these measurements (92%) were on Fin Whales, but included 27 values for Blue Whales and 14 for Humpback Whales.

The observations of Addison represent a beautiful series of data to show how constant the body temperature can be in whales (Table IV). The number of these measurements (490) is more than three times that of all the other values identified in the literature. In these measurements on muscles from animals which reached the factory ship at times ranging from one to seventeen hours after death, no fall in temperature at all was seen and actually a small increase $(0.033^{\circ} \text{ C./hr.})$ was observed. This sequence also involved the transition through rigor from "dry" meat to "wet" meat, and the increase of 0.6° C. in temperature is attributable to the breakdown of the phosphate energy reserve in the muscle. When values for "wet" and "dry" meat were plotted separately, neither showed any change in temperature with time.

The range of observed values in this series (89–101° F. or 31.7–38.3° C.) seems large but only reflects the large sample size. A frequency polygon of these



FIGURE 6. Frequency distribution polygon for *longissimus dorsi* temperatures from data of F. A. Addison (personal communication from J. G. Sharp). Heavy curve, all values; dotted curve, "dry" meat (before *rigor*); dashed curve, "wet" meat (after *rigor*): ± 1 S. D. = 68%; ± 2 S. D. = 94%; ± 3 S. D. = 99.6%. The terms "dry" and "wet" are practical expressions describing meat which is respectively firm and sticky (before *rigor*) or wet and sloppy (after *rigor*) to the touch. A third term, "rubbery," relates to muscle actually in *rigor mortis* (Sharp and Marsh, 1953).

data is given in Figure 6 for the total data as well as for the "wet" and "dry" samples. This transformation has an evident, but lesser, influence on the spread of the data, the principal variability being, apparently, differences in initial temperatures in the whales. The standard deviation of the values, 0.9°, represents considerable variation but not more than is seen in many other mammals.

The data of Zenkovic (1938) are of particular interest because he measured five different species and further was able to make observations on five individuals which were still alive, although seriously wounded. Because this paper is difficult of access, the results are summarized in Table V. Ordinarily, values from living animals would be given precedence over values from dead animals. But we have just considered this problem at length to conclude that in the whale this is not so. However, Zenkovic's five values on still living animals are distinctly higher than his other values, including one taken less than an hour after death. Our best judgment is that these "live" values are not representative, but are the result of the continuing exertions of the mortally wounded whale, which is, of course, only approached when it has been completely exhausted and is almost dead. This is not to say that these temperature levels are necessarily outside the normal distribu-

	1		1	1			
Hours after death	Sperm	Grey	Fin	Humpback	Blue	Mean	Hours after death
0	38.2 (2)		38.4(2)	38.1(1)		38.3 (5)	0
<u>1</u> -1	0012 (2)	36.5 (3)				36.7(12)	1 11
$1 - 1 \frac{1}{2}$		36.4 (6)	37.1 (3)			00.7(12)	2 1 2
$1\frac{1}{2}-2$	36.7 (3)			36,3(4)		36.5(12)	11-4
$\tilde{2}-3$		36.6 (3)					
3-4			36.2 (2)				
$5 - 7\frac{1}{2}$	35.5 (6)					35.9 (9)	5-9
$7\frac{1}{2}-9$		36.3 (3)					
9-13			35.5 (3)				
12-16					35.7(3)	35.6 (6)	9-16
$0 < T_p \ge 4$	367 (3)	36.6(12)	36.8 (5)	36 3(1)		36 6(24)	
$O < T_B < T_D$	35.9 (9)	36 5(15)	36.3 (8)	36.3(1)	35 7 (3)	36.2(30)	
$T \equiv 1$	27 2 (5)	26 6(12)	272(7)	26.7(5)	00.7(0)	26 0(20)	
1 B < 4	37.3 (3)	30.0(12)	31.3 (1)	30.7(5)	25 5 (2)	30.9(29)	
mean I _B	30.3(11)	30.5(15)	30.7(10)	30.7(5)	35.7(3)	30.1(44)	
	1	1				1	·

TABLE V Whale temperatures from Zenkovic (1938)*

* "For live whales, insertion was either in the animals side nearer the belly, almost at the beginning of the whales side folds; or sometimes in the belly depending on the position in which the whale was made fast to the boat."

"Thermometer No. 2 was completely immersed to a depth of 30–40 cm in the body and extracted with a line of veins. The thermometers were kept in the animals body for 10 minutes".

TABLE VI

Whale temperatures by M. Nishiwaki*

Species	Sex	Length ft.	Chase hr.	Hours post- mortem	T _B ** (Range)	#
Blue	്	75-79		<1	33(30-36)	6
	ę	70-87		<1	31(27-35)	7
Fin	ី	62-71		<1	29(25-31)	6
	ę	67-74		<1	32(29-36)	5
				< 0.1	31.0(25-36)	21
			< 0.2	< 0.3	29(25-34)	7
			0.25	< 0.3	33(30-35)	3
			0.5	< 0.3	32(29-35)	4
			1-2	< 0.3	32(30-35)	3
			5	< 0.3	36	1

* Taken during the Japanese Antarctic Whaling Expedition, 1948-49 (personal communication).

** Values represent measurements in which a thermometer probe was inserted 60-70 cm. $(2\frac{1}{2} \text{ ft.})$ into the "trunk, the portion immediately below the base of the flipper." "It is, therefore, probable that the bulb rested in the abdominal cavity in some of the measurements." In five individuals "trunk" values averaged 4° higher than "tail" values in which "the bulb of the thermometer was forced 40-50 cm. $(1\frac{1}{2} \text{ ft.})$ into the portion of the lateral side of the whole body below the dorsal fin."

tion for whales, since Addison's range of values went as high as 38°. We could, then, take this as an example of the effect of vigorous activity on body temperature in the whale, but would not accept these values as representative of the average temperature in this animal.

Nishiwaki's data (Table VI) may also be looked at in this regard. Comparison of animals chased for times ranging from ten minutes up to five hours suggests some increase, but the variability is too great for conviction. And, of course, an animal could well reflect considerable prior activity, even though it were chased for only a short time. In both these studies average values for the several species showed no significant differences, nor were differences due to sex or size apparent.

Whale temperatures from all available sources are summarized in Table VII and average 35.4° C. for twelve authors. The greater number of these values were specifically taken in the dorsal musculature and average 34.6° C. for 547 individuals (34.5° C. for eight authors). This is a distinctly lower mean than that of the residual group which includes the present study, 36.2° C. for 57 individuals (36.9 for four authors). This suggests that, although consistent high values are found in the back muscle, it is not the warmest spot in the whale body. In the porpoise (*Delphinus*), Richard and Neuville (1897) found the viscera to be 0.3° C. warmer than the dorsal muscle mass.

This overall mean value of 35.4° C., or even the latter mean of 36.2° C. for

Observer	Species	Hours dead	Тв °С.	Values	Location
Scoresby, 1820	Bowhead		38.8	(1)	Blood
Guldberg, 1900	(Sperm)*		(40.0)*		
Guldberg, 1885	Blue	2	35.4	(1)	"Back flesh"
Laurie, 1933	Blue, fin		35.1	(30)	Long. dorsi
Zenkovic, 1938	Humpback, fin,	1-16	36.2	(35)	
	sperm, blue gray			()	
	Humpback, fin,	alive	(38.3)	(5)	
Aaser 1911	sperm	1-24	33.1	(18)	Inside muscle
Parry 1949	Blue	1	35.5	(10)	Epaxial muscle
Cockrill 1951	Ditte	1	(31 - 34 5)	(0)	$9^{\prime\prime}$ in fillet
Robinson <i>et al</i> 1953	Blue fin	0-24	33.4	(26)	Inside muscle
Kanwisher and	Fin		36.6	(1)	Muse and body
Leivestad, 1957	1		00.0	(-)	cavity
Addison**	Fin	1-16	34.7	(490)	Long. dorsi
Ash**		-15	35	(1)	Long. dorsi
Nishiwaki**	Blue, fin	1	(25-36)	(24)	0
Sharp**		0.4	34.4	(1)	Long. dorsi
This study	Humpback	0.5-18	36.0	(20)	See text
	·				

TABLE VII

A	verage i	body	tempe	ratures	in what	les, af	fter vari	ious o	bservers
---	----------	------	-------	---------	---------	---------	-----------	--------	----------

* Guldberg (1900) cited Beal (1839) for this value and species, but Beal only refers to this value as an upper limit for cetaceans. Desmoulins (1822), whom Beal cited for his statement, apparently arrived at the value of 40° C. by arbitrarily adding on $1-4^{\circ}$ C. for presumed cooling to the values of Scoresby (1820) for a narwhale and a baleen whale (Tables VII and VIII).

** Personal communication.

whales, is well below the averages of 37.8° C. for 56 temperate mammal species (Morrison and Ryser, 1952) and of 38.3 for 21 Alaskan mammal species (Irving and Krogh, 1954). It is of interest to see if this is also true of smaller cetaceans, *i.e.*, whether the low body temperature relates to the large size or to the order of Cetacea. Table VIII summarizes the temperatures available for smaller cetaceans. Values from nine authors range from 35.6 to 37.8° C, and average 36.5° C. (36.7 for 13 individuals). It might be suggested that abnormally high values

Reference	Species	Тв in °C.*	Site	Notes
Richer (1672)	marsoüin	"Scarcely less warm than land ani- mals"**	Abdomen	
Boerhaave (1741)***	fishes with lungs	"As other mammals"		
Broussonet (1785)	marsoüin	35.6†	Neck wound	Bleeding heavily
Scoresby (1820)	Monodon monoceros	36.1	"Blood"	15'; dead 90 min.
Davy (1826)	porpoise	37.8	Liver	Live on deck, at lat. 8°
Richard and Neuville (1897)	Delphinus delphis	35.6 (35.3)	Rectum, ab- domen Dorsal muscle mass	Harpooned
Grieg (1907)	Orcinus gladiator	37.1*	Muscle	Harpooned, dragged on shore
Portier (1908)	Orcinus gladiator	36.6 (36.9)	Rectum, liver, vagina Brain	
Jolyet (1893)††	Tursiops truncatus	37.0		
Wislocki (1933)	Tursiops truncatus	36.0		Stranded (?)
Woolsey†††	Tursiops truncatus	37.0	Rectum	Restrained out of water for 2 hrs.

TABLE VIII The body temperature of some smaller cetaceans†

‡ Early interest in the temperature of aquatic mammals is notable. Martine (1740), who has been cited as the first reliable authority in medical thermometry, devoted more space to this group than to all the other homeotherms except man.

- †† Not clear if this is an original measurement.
- ††† Personal communication.

166

^{*} All values represent single individuals except Grieg (=5).

^{**} Apparently no thermometer used.

^{***} Probably not an original observation.

[†] Calculated from original value of 28.5 taken as °R.

will be obtained from cetaceans restrained out of water. If the three such references are eliminated, the average for the remainder is 36.2° C. (six authors and individuals).

We might look for a more general correlation of low body temperature with an aquatic mode of life. Values in Table IX for two carnivores average 37.2 (12 individuals) and for seven pinnipeds average 37.3 (70 individuals). These means are closer to the general averages for mammals but are, however, distinctly below a mean value of about 38.5° C. for their terrestrial relatives in the Carnivora which have higher-than-average body temperatures (Morrison and Ryser, 1952; Irving and Krogh, 1954). One further specific comparison of interest relates the marine polar bear to its terrestrial relatives. Twelve values for black and

Species	T _B in °C.	Site	Author
"Sea Calf"	(38.9)	abdomen	Martine (1740)
Phoca vitulina	37.8 (24:3)*	liver, abd.	Scholander et al. (1942)
	(38.4) (7:2)	brain	
Erignathus barbatus	37.2 (5:5)††	rectal	Irving and Krogh (1954)
Halichoerus grypus	36.5 (6:1)		Scholander (1940)
Mirounga angustirostris	36.0 (13:13)***	rectal	Bartholomew (1954)
Mirounga leonina	37.8		Aretas (1951)
Callorhinus ursinus	37.4 (32:32)	heart	Hanna (1924)
Callorhinus ursinus	37.7 (13:13)**		Bartholomew and Wilke (1956)
Eumetopias jubata	38.5 (2:2)†	rectal	lrving and Krogh (1954)
Enhydra lutris	38.5 (1:1)	rectal	Irving and Krogh (1954)
Enhydra lutris	36.8 (6:6)†		Stullken and Kirkpatrick (1955)
Thalarctos maritimus	37.5 (3:3)†		Anon. (1827)
Thalarctos maritimus	37.3 (2:2)†	viscera	Irving and Krogh (1954)

TABLE IX

Body temperatures in marine Carnivora and Pinnipedia

* Lost 2.5° during dive; parenthesized numbers show measurements and individuals.

** Gained up to 4° during activity on land.

*** Lost 2.2° at night (5:5).

† Shot.

brown bears average 37.9° C. or 0.5° C. above the level of the polar bear (Irving and Krogh, 1954; Hock, 1957). Although the difference is small, it appears statistically significant (t = 3.0). In sum, therefore, all of these group means do support the association of aquatic life with a reduction in body temperature.

SUMMARY

1. A series of some 250 body temperature measurements were made on 20 humpback whales (*Megaptera novaeangliae*) from the east coast of Australia. The distribution in the animal was plotted by means of a series of ventro-dorsal temperature profiles. Inverted temperature profiles were sometimes found, indicating the presence of internal masses of cold water and offering an explanation for the aberrant temperature values sometimes reported for whales.

2. Maximum values were found posteriorly near the umbilicus and the genital

opening, and at a depth of 3.3 feet. The average was 36.0° ; and there was no correlation with sex, size (33–40 ft.), or time after death (0.5–18 hrs.). This body temperature is close to the mean of literature values for whales (35.8°) and, as well, for smaller cetaceans (36.4°), but is appreciably below that for the Pinnipedia (37.3°).

LITERATURE CITED

- AASER, C. S. S., 1944. Rapport over hvalkjøttundersøkelser sommeren 1943. Norsk. Vct. Tidsskr., 56: 33-62.
- ANON., 1827. Temperature de quelques Animaux du Nord, prises au Port Bowen (Extrait du dernier Voyage du Capitaine Parry). Ann. de Chim. et de Phys. (2nd ser.), 34: 111.

ARETAS, R., 1951. L'éléphant de mer (*Mirounga lconina* (L)). *Mammalia*, 15:105–117. BARTHOLOMEW, G. A., JR., 1954. Body temperature and respiratory and heart rates in the

northern elephant seal. J. Mamm., 35: 211–218. BARTHOLOMEW, G. A., AND F. WILKE, 1956. Body temperature in the northern fur seal, Callorhinus ursinus. J. Mamm., 37: 327–337.

BEALE, T., 1839. The Natural History of the Sperm Whale. Van Voorst, London. 393 pp.

- BENEDICT, F. G., 1936. The physiology of the elephant. Carnegie Institution of Washington. Publication No. 474. 302 pp.
- BOERHAAVE, H., 1741. Elementa Chemiae, 2d ed. (translated by Peter Shaw from original Latin). Longman, London.

BROUSSONET, 1785. Mémoire pour servir à l'histoire de la respiration des poissons. Mém. (de Mathématique et de Physique) de l'Acad. Roy. des Sci., Paris, 174-196.

COCKRILL, W. R., 1951. Antarctic pelagic whaling. Vet. Rec., 63: 111-124.

DAVY, J., 1826. Observations on the temperature of man and other animals. III. Of the temperature of different kinds of animals. *Edin. Phil. J.*, **14**: 38-46.

DESMOULINS, A., 1822. Dict. class. d'Hist. Nat., 2: 159.

GRIEG, J., 1907. Hvalernes legemstemperature. Naturen, 31: 125-126.

GULDBERG, G. A., 1885. Über das Centralnervensystem der Bartenwale. Forhandlinger i Videnskabs-selskabet i, Christiania, Aar 1885, No. 4. 154 pp.

GULDBERG, G. A., 1900. Nyt magazin for naturvidenskaberne, 38: 65-70.

HANNA, G. D., 1924. Temperature records of Alaska fur seals. Amer. J. Physiol., 68: 52-53.

- Hock, R. J., 1957. Hilbernation in Cold Injury. Trans. 5th Conf. Josiah Macy Found., pp. 61–133.
- IRVING, L., AND J. KROGH, 1954. Body temperatures of arctic and subarctic birds and mammals. J. Appl. Physiol., 6: 667-680.

JOLYET, F., 1893. Recherches sur la respiration des cétacés. C. R. Soc. Biol., 45: 655-656.

- KANWISHER, J., AND H. LEIVESTAD, 1957. Thermal regulation in whales. Norwegian Whaling Gazette, 46: 1-5.
- LAURIE, A. H., 1933. Some aspects of respiration in blue and fin whales. Discovery Reports, 7: 363-406.

MARTINE, 1740. Essays Medical and Philosophical. A. Millar, London. 376 pp.

- MORRISON, P. R., AND F. A. RYSER, 1952. Weight and body temperatures in mammals. Science, 116: 231-232.
- PARRY, D. A., 1949. The structure of whale blubber, and a discussion of its thermal properties. Quart. J. Micr. Sci., 90: 13-25.
- PORTIER, P., 1908. Température de vertébrés marins, en particular des poissons du groupe des thons. C. R. Soc. Biol., 64: 400-402.
- RICHARD, J., AND H. NEUVILLE, 1897. Sur quelques cétacés observés pendant les campagnes du yacht Princess-Alice. Mém. Soc. Zool. de France, 10: 100-109.
- RICHER, —, 1672. Observations astronomiques et physiques faites en l'isle de Caïenne. Mem. Acad. Sci., 7: 230-326.
- ROBINSON, R. H. M., M. INGRAM, R. A. M. CASE AND J. G. BENSTEAD, 1953. Whalemeat: Bacteriology and Hygiene. Dept. Sci. and Indust. Res., Food Invest. Special Report No. 59. London. 56 pp.

SCHOLANDER, P. F., 1940. Experimental investigation on the respiratory function in diving

Scholander, P. F., L. IRVING AND S. W. GRINNELL, 1942. On the temperature and metabolism of the seal during diving. J. Cell. Comp. Physiol., 19: 67-78.
 SCHOLANDER, P. F., AND W. E. SCHEVILL, 1955. Countercurrent vascular heat exchange in the fins of whales. J. Appl. Physiol., 8: 279-282.

SCORESBY, W., 1820. An account of the arctic regions. Constable, Edinburgh, 1: 477.

SHARP, J. G., AND B. B. MARSH, 1953. Whalemeat: Production and Preservation. Dept. Sci. and Indust. Res., Food Invest. Special Report No. 58. London. 47 pp.

STULLKEN, D. E., AND C. M. KIRKPATRICK, 1955. Physiological investigation of captivity mortality in the sea otter (Enhydris lutris). Transactions of the Twentieth N. Amer. Wildlife Conference, 476-494.

WISLOCKI, G. B., 1933. Location of the testes and body temperature in mammals. Quart. Rev. Biol., 8: 385-396.

ZENKOVIC, B. A., 1938. The temperature of whales. C. R. de l'Acad. des Sci. de l'URSS, 18: 685-687.